

'Business as usual': drilling predation across the K-Pg mass extinction event in Antarctica

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ABSTRACT

A survey of 759 predatory drill holes in Late Cretaceous and Paleogene molluscan and serpulid worm prey from Seymour Island (Antarctica) has allowed exploration of the effects of the K-Pg mass extinction on predator-prey dynamics at this high latitude site. Circular holes (0.62 - 6.41 mm in diameter), suggesting a large gastropod predator, most probably "*Vanikoropsis*" *arktowskiana*, occur throughout the study interval. Analysis suggests that the driller was a catholic predator capable of attacking a range of prey types, showing some degree of size and stereotypic handling behaviour. Although there were changes in prey choice across the extinction event, these reflect changes in available prey, and in particular limited options immediately post extinction. There were no significant changes in failure rate (Prey Effectiveness) over the mass extinction. Our findings suggest that at this site, for this particular predator, aside from menu choice, predation dynamics post-extinction was 'business as usual'.

1. Introduction

Predators are thought to have played a fundamental role in shaping the course of evolution of their prey (Vermeij, 1987; Stanley 2008). It is clear that the dynamics between predators and prey have not been constant over the Phanerozoic. Vermeij (1987) hypothesised that mass extinctions perturb these dynamics and, in particular, predicted that these events selectively remove more escalated (i.e. better defended) prey. These ideas have been tested for post-Palaeozoic extinction events, most notably the Cretaceous-Paleogene (K-Pg) and Eocene-Oligocene events, based on patterns of drilling predation in molluscan prey from the US Coastal Plain (Hansen and Kelley, 1995; Hansen et al. 1999;

Hansen et al 2004; Kelley and Hansen, 1993, 1996a,b, 2006; Kelley et al., 2001; Reinhold and Kelley, 2005). These studies show a series of escalation cycles from the Cretaceous onwards punctuated by significantly higher frequencies of drilling after mass extinction events. These authors follow Vermeij (1987) in proposing that an increase in the frequency of drilling predation in recovery faunas is due to the selective removal of escalated prey taxa, but supporting evidence for this hypothesis, as expressed by prey morphology, is limited (Hansen *et al.*, 1999; Reinhold and Kelley, 2005). In addition, specific studies of the metrics of prey effectiveness have not supported the notion that predators were more successful in the immediate aftermath of extinction events (Kelley et al., 2001; 2006).

Mallick et al. (2014, p. 227) suggest that the effects of mass extinction on the dynamics of drilling predation 'should be global'. However, this seems unlikely to be true. Mass extinctions are widespread phenomena to which there are local responses. The US Coastal Plain faunas are relatively low latitude, mixed carbonate - clastic shelf communities, which were sited in close proximity to the Chicxulub impact site, the postulated cause of the K-Pg event (Schulte et al., 2010). There have been few other detailed studies which have attempted to test the effects of mass extinction at different sites, although two recent papers examine drilling predation associated with the K-Pg event in India (Mallick et al., 2013; Mallick et al., 2014), another low latitude, subtropical site in close proximity to the Deccan Traps, which is another possible extinction trigger (Keller, 2005). These studies demonstrated high frequencies of drilling predation in turritellid prey below the boundary but found no evidence of any drill holes in the relatively small sample from the sparse fauna above it, although it seems unclear what the significance of the latter is.

Not all regions exhibited similar levels of extinctions in the wake of the K-Pg event, with higher latitudes apparently least affected (Zinsmeister et al., 1989; Keller, 1993; Raup and Jablonski, 1993). It is possible that environmental variation associated with a strongly seasonal climate may have less influence at higher latitudes, where more generalist faunas prevail (Alegret et al., 2012). Additionally, following the meteorite impact or Deccan volcanism hypotheses, the effects of such an event are likely to be more significant closest to the site of impact/eruption (Raup and Jablonski, 1993; Schulte et al., 2010). It is also evident that patterns of predator-prey interactions are naturally highly variable on both temporal and spatial scales in both modern (Schmidt, 1989; Cadée et al., 1997; Harper and Peck 2016) and fossil faunas (Hansen and Kelley, 1995; Harries and Schopf, 2007). Clearly, additional studies are needed which investigate a broader range of environments and palaeolatitudes in order for us to capture a full sense of the variability between sites and so to fully unravel the role of mass extinction events in predator- prey relationships.

Recognising and measuring the activities of predators from the fossil record is highly problematic (Bromley, 1981; Harper, 2016). However, predators, such as gastropods or octopods, which leave sharp-sided circular drill holes provide less ambiguous and more preservable evidence of their activities than do many other predators, and offer the opportunity to examine frequency, success and prey selectivity (Kelley and Hansen, 2003; Harper, 2003). As such they have been a key method of assessing various predation-based hypotheses (Leighton and Aronowsky, 2003; Huntley and Kowalewski, 2007; Klompmaker et al., 2017). In this paper we investigate drilling predation on a range of molluscan and serpulid worm prey over the K-Pg boundary at a high palaeolatitude ($\sim 65^{\circ}\text{S}$) site on Seymour Island near the northern end of the Antarctic Peninsula. Our aim is to survey a variety of

79 prey taxa, consider possible culprits, and use various analyses of the drill holes themselves
80 to test the following hypotheses based on the predictions of Vermeij (1987, 1995) and Kelley
81 *et al.* (2001):

- 82 - Prey effectiveness decreases after mass extinction events as indicated by a decrease
83 in both incomplete drill holes and multiply drilled individuals.
- 84 - Predators become less selective after mass extinction as evidenced by reduced
85 stereotyped handling patterns and poor size selectivity

86

87 **2. Geological setting**

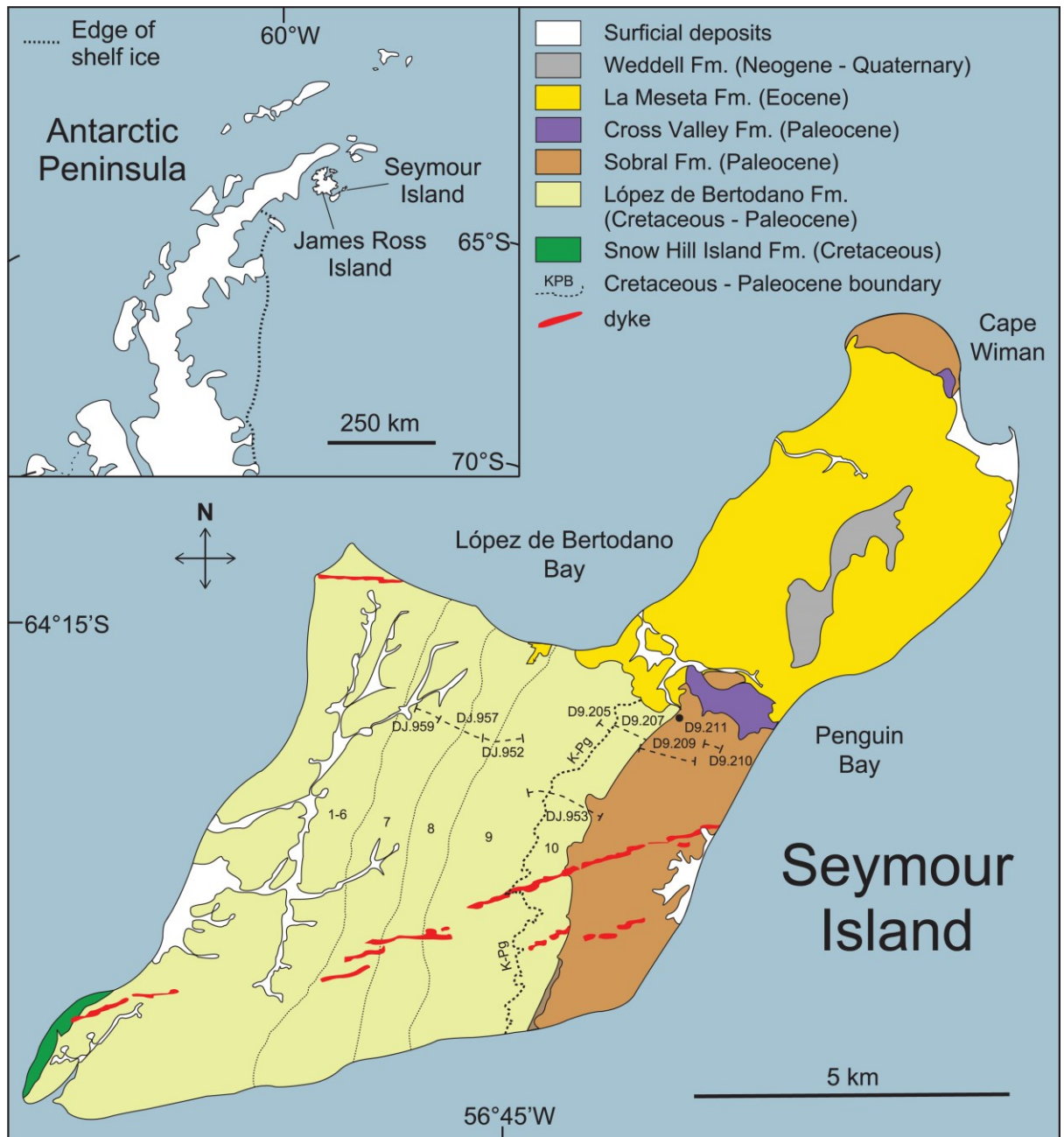


Fig. 1. Geological and locality map for Seymour Island, north-eastern Antarctic Peninsula. Key section lines are marked, together with localities that are prefixed by the letters “D” or “DJ”. Also shown are the main informal lithostratigraphical divisions for the López de Bertodano Formation. 1-9 refer to units Klb 1-9 within the Cretaceous López de Bertodano Formation and 10 to unit Kplb 10 above the K-Pg boundary. Based on Crame et al. (2014, fig. 1), with minor modifications

The Seymour Island K–Pg sedimentary succession is part of an extensive back-arc basin exposed on the north-eastern flank of the Antarctic Peninsula (Hathway, 2000) (Fig. 1).

In the central and southern parts of the island, a 950m-thick sequence of uppermost Cretaceous (Maastrichtian) silty mudstones, siltstones, and fine- to coarse-grained sandstones dips gently eastwards beneath a 300m-thick sequence of very similar Paleocene lithologies (Sadler, 1988; Montes et al., 2010; Bowman et al., 2012). As it has so far proved impossible to subdivide the Maastrichtian succession into meaningful lithostratigraphic units, we have retained the use of the informal mapping divisions proposed by Sadler (1988). The most fossiliferous intervals occur in units Klb 7-9, i.e. approximately the uppermost 500 m of Maastrichtian sediments, where there is a rich ammonite – bivalve assemblage, together with other macrofossil taxa such as gastropods, echinoids, decapod crustaceans and serpulid worms (Fig. 1) (Macellari, 1988; Zinsmeister et al., 1989; Feldman et al., 1993; Zinsmeister, 2001; Olivero, 2012). The Maastrichtian stratigraphy of Antarctica is definitively defined in Crame et al. (2004) and detailed stratigraphic columns for the K – Pg succession are shown in Crame et al. (2004), Bowman et al. (2014), Kemp et al. (2014) and Witts et al. (2015, 2016), including the locality information and assignment to biostratigraphic zone for the samples used in the current study (Crame et al. 2004; Figures 2 and 4).

The base of section DJ. 959 occurs in the lower levels of unit Klb 7, approximately 450m beneath the K–Pg boundary. It is marked by the sudden incoming of the ammonites *Kitchinites darwini* and *Grossouvrites gemmatus*, together with a prolific benthic macrofauna (Crame et al., 2004). The boundary between units Klb 7 and Klb 8 is transitional but at a level of approximately 200m beneath the K–Pg boundary the base of Klb 9 is marked by the sudden appearance of medium – large pachydiscid ammonites attributable to *Pachydiscus riccardi* and *Pachydiscus ultimus*. These two species have been referred to an

informal *P. riccardi* – *P. ultimus* horizon (or zone) which overlies a *Pachydiscus ootacodensis* horizon (Olivero and Medina, 2000; Crame et al., 2004). Locality DJ. 957 is equivalent to the upper levels of Klb 7 and the greater part of Klb 8; DJ. 952 is equivalent to most of Klb 9, but the uppermost levels, including the K – Pg boundary, are included in DJ. 953, which extends into the basal Paleocene Sobral Formation (Fig. 1).

The K–Pg boundary occurs at the junction between units Klb 9 and Kplb 10 and is marked by a prominent 5–6 m scarp of greenish-weathering glauconitic sandstones that can be traced for some 7 km across the island. At the crest of the scarp is a 1 m-thick, sharp-based concretionary glauconite that is equivalent to Zinsmeister's (1998) Lower Glauconite; it is the base of this bed that corresponds to the last ammonite occurrence and a small Iridium anomaly (Elliot *et al.*, 1994), and is here taken as the K – Pg boundary (Fig. 1). Directly above the Lower Glauconite is a 2–3 m sequence of yellowish to tan-weathering siltstones and fine sandstones devoid of any obvious macrofossils apart from scattered fish fragments, including various aggregations of scales, bones and teeth. This is the so-called fish-kill horizon and is directly overlaid by a second prominent glauconitic sandstone identified as the Upper Glauconite (Zinsmeister, 1998). Detailed macrofossil investigations across the K–Pg boundary indicate species level extinctions in the region of 60% and genus levels of 30 – 40% (Witts et al., 2015, 2016). Such levels are similar to those seen at much lower latitudes and attest to a rapid and severe global extinction event.

Directly overlying the Upper Glauconite there is a subtle change in lithologies to massive grey – brown mudstones and muddy siltstones containing numerous small concretions. But what is even more striking is the change in benthic faunas. Serpulid worm tubes and cidaroid spines, both abundant throughout the latest Maastrichtian, are

completely absent and the molluscan macrofauna is dominated by a small number of extremely abundant species; the shallow-burrowing bivalves *Lahillia larseni* and *Cucullaea ellioti*, and epifaunal gastropod, *Struthiochenopus hurleyi*, are particularly abundant (Crame et al., 2004; Stilwell et al., 2004). These appear to be opportunist species in the wake of the mass extinction, and this 55 – 60 m thick interval (unit Kplb 10 of the López de Bertodano Formation) is referred to informally as the “recovery interval” (localities DJ. 953 and D9. 207, Fig. 1).

A low-angle but distinct unconformity separates the top of unit Kplb 10 from the base of the overlying Sobral Formation (Fig. 1). The latter comprises approximately 300 m of mudstones, silty mudstones and sandstones with a characteristic greenish weathering tinge (localities D9. 209 and D9. 210, Fig. 1). Macrofossils reoccur in some abundance at the 48 – 120 m level in the Sobral Formation and are dated as earliest Danian (i.e. ~65 Ma; Bowman et al., 2012, 2016). Thereafter the relative scarcity of macrofossils is related to a marked change in sedimentary facies, with a distinctive set of sandstones between 185 – 230 m showing the characteristic features of tidal sandbars. A sparse macrofauna from the very highest levels of the Sobral Formation is dated as Danian – Selandian boundary (i.e. ~61 Ma; Montes et al. 2010; Bowman et al., 2016).

3. Materials and methods

This study used specimens that were collected over three field seasons by BAS staff and their collaborators in a comprehensive programme to investigate the biostratigraphy and palaeoecology of the Antarctic K-Pg sections on Seymour Island. The sampling strategy is as given in Witts et al. (2016). In brief, very detailed macrofossil collections were made up the various stratigraphic sections. In practice this involved the use of some 377 individual

sampling stations where work continued at each one until a representative collection, i.e. when all the obvious macrofossil types had been obtained. Stratigraphic sections across Seymour Island were correlated using a variety of palaeontological and lithological criteria (Crame et al., 2004; Bowman et al., 2012, 2016; Witts et al., 2015, 2016). Accurate taxonomic identifications were made in the laboratories of the British Antarctic Survey, Cambridge (BAS) and the University of Leeds (UK), and further material was examined in the Zinsmeister Collection housed at Paleontological Research Institute (Ithaca, USA) (Zinsmeister and Macellari 1988; Stillwell et al. 2004). Crame et al. (2014) provided a detailed discussion of taxonomic affinities. As the field collections were made for a different set of studies (Bowman et al. (2014), Kemp et al. (2014) and Witts et al. (2015, 2016)) with different aims, specimens were collected without bias with regard of drill holes.

All molluscan specimens in the three repositories were screened for predatory drill holes (around 8,000 specimens), and at BAS and Leeds all serpulid worms were also included (around 2,500 individuals). In practice most of these specimens had been cleaned previously and were largely free of matrix. Each specimen was examined carefully, using a stereomicroscope as required. Predatory drill holes were recognized using the criteria developed by Baumiller (1990), though relaxing the need for evidence of stereotypic positioning (Harper, 2003). All measurements were made with vernier calipers. In view of the large sample size and the fact that we had chosen not to calculate drilling frequency (see Discussion) we did not record data for undrilled specimens. For each drilled individual specimen the following information was recorded: taxon, size of the prey (to the nearest 0.1 mm) according to taxon dependent parameters (length or height for bivalves as appropriate, length for gastropods and width for serpulids) and, for bivalves, the state of articulation, and

190 the number of drill holes present. A conservative approach was adopted such that doubtful
191 drill holes, which may have been genuine but altered by taphonomic processes, were
192 discounted from the analysis. For each drill hole, outer diameter (measured to the nearest
193 0.01 mm), shape and positioning were recorded and an assessment made as to whether
194 they were complete (i.e., penetrate the full thickness of the shell) or incomplete (i.e.,
195 terminating within the thickness of the shell rather than fully perforating it). Following the
196 objection laid out by Harper (1994), no attempt was made to distinguish between functional
197 and non-functional drill holes using the ratio of outer and inner diameters as advocated by
198 Kitchell et al. (1986). Drill hole positioning was plotted on a master diagram for each prey
199 taxon using the centre of the hole. For bivalves, holes were recorded as penetrating either
200 left or right valves and also which of four approximately equal area sectors on each valve
201 (dividing each valve into posterior and anterior sections, each themselves divided into
202 dorsal and ventral areas). Similarly, drill hole positioning on gastropod prey was recorded as
203 either dorsal or ventral, with note made of the position of perforation relative to the
204 aperture, and also position along the spire, while those on serpulid worms were recorded as
205 puncturing one of 8 even area radial sectors relative to the aperture and also dorsal or
206 ventral halves. The coiled nature of both gastropods and serpulids gives a measure of
207 uncertainty in spatial analysis where the aperture is damaged and also where an incomplete
208 drill hole's relative position may have changed markedly if it significantly pre-dated the
209 death of the prey. All spatial analyses were assessed by chi-squared test, and null
210 hypotheses which predicted random siting of drill holes leading to equal distribution over all
211 sectors.

Relative values of prey defence were calculated using the Prey Effectiveness (PE) metric proposed by Vermeij (1987), defined as the number of incomplete drill holes in a sample divided by the total number of drill holes present. Where it was not possible to determine whether the hole was complete or not (because they were filled with indurated sediment), these specimens were not included. PE was calculated for individual species in instances where the number of holes exceeded 10. We also calculated an index for multiple drill holes used by Kelley and Hansen (1993) and subsequently defined as MULT by Kelley et al. (2001) as a complementary measure of prey effectiveness. MULT is determined by the number of holes in multiply drilled specimens divided by the total number of attempted drill holes in a particular taxon. It is difficult to make meaningful estimates of MULT for bivalve taxa where there is a tendency for valves to be disarticulated. Nevertheless, most *Lahillia* and arcoids were articulated and the tendency for drilling left valves of oysters makes some estimates feasible from the material available. Additionally for each multiple-drilled individual we tabulated the complete/incomplete status of each hole within the multiple set.

Data were split into four consecutive time intervals. Below the K-Pg event we used the ammonite zones recognised by Crame et al. (2004) namely, the *ootacodensis* Zone (equivalent to Klb 7 and 8) and the *ultimus/riccardi* Zones (Klb 9), to divide the top part of the López de Bertodano Formation. Above the boundary data were split between unit Kplb 10 (the recovery interval), and the succeeding Sobral Formation. Where data permitted we tested for differences between the four identified intervals but where insufficient we amalgamated the *ootacodensis* and *ultimus/riccardi* Zones (i.e. Klb 7-9) to provide a single pre-extinction dataset.

4. Results

In total we recorded 759 drill holes in a range of molluscan and serpulid worm prey taxa (Fig. 2) and distributed throughout the sequence. A summary of these data is presented in Table 1. As discussed in Section 5.4, we chose not to calculate drilling frequencies for the molluscan prey taxa because of the nature of the samples available. These data were available for the serpulid taxa where the frequencies of individuals with at least one drill hole were 5.7% (N = 1663 individuals) and 6.6% (N=786 individuals) for Klb 7 and 8 and Klb 9 respectively.

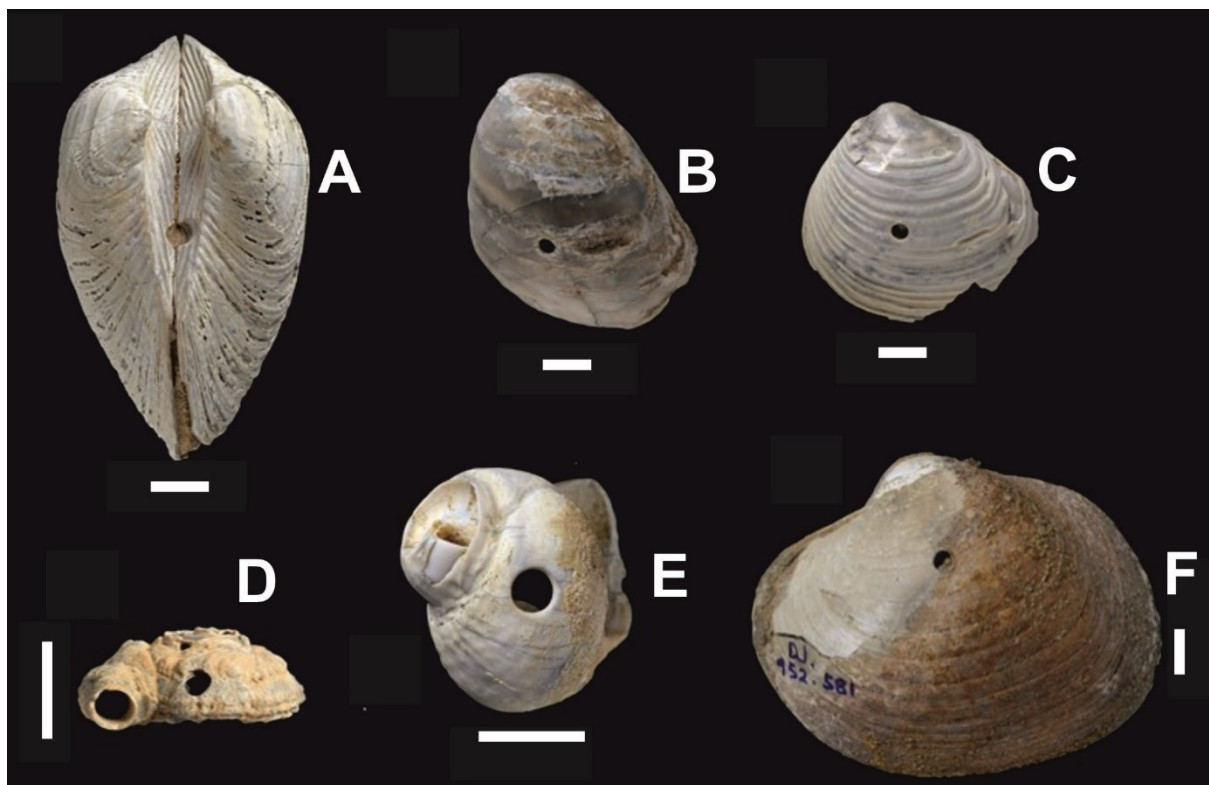


Fig. 2. Examples of drilled prey. A, *Cucullaea antarctica* (DJ.959.141, Klb 7 and 8); B. *Pycnodonte vesicularis* (DJ.953.627, Klb 9); C. *Eselaevitrigonia regina* (DJ.957.365, Klb 8); D. *Rotularia* sp. (DJ.952. A2, Klb 9); E. “*Vanikoropsis*” *arktowskiana* (DJ.951.28, Klb 8) and F, *Lahillia larseni* (DJ.952.581, Klb 9). All scale bars represent 10 mm. All specimens in BAS Collections, Cambridge UK.

249 **Table 1.** Incidence of drill holes in molluscan and serpulid prey.

Prey	Number of drill holes	Number of failed drill holes	Prey Effectiveness [^]	Range of drill hole diameters (mm)	Number of multiply drilled individuos [MULT] [†]
Sobral Fm					
Gastropods <i>Struthiochenopus nordenskjoldi</i> / <i>hurleyi</i> *	25	5	0.200	0.71-4.13	5 (11) [0.44]
" <i>Vanikoropsis</i> " <i>arktowskiana</i>	4	0	-	1.10-2.77	1 (2)
Bivalves <i>Cucullaea ellioti</i>	1	0	-	2.92	0
<i>Pycnodonte seymourensis</i>	7	5	-	1.79-4.68	2(6) [0.86]
Venerid indet.	3	0	-	2.14-3.15	0
<i>Lahillia huberi</i>	2	0	-	3.26-4.35	1 (2)
<i>Saxolucina antarctipleura</i>	2	0	-	0.96-1.04	0
Paleogene (UKplb 10) (López de Bertodano Fm)					
Gastropods <i>Struthiochenopus nordenskjoldi</i> / <i>hurleyi</i> *	14	1	0.071	1.01-2.89	1(2) [0.143]
Bivalves <i>Cucullaea ellioti</i>	3	2	-	2.46-2.91	0
<i>Lahillia larseni</i>	27	4	0.148	2.09-4.98	5 (10) [0.370]
Serpulids <i>Rotularia (Austrorotularia)</i> sp.*	6	3	-	0.63-1.26	2(6) [1.00]
K-Pg boundary here					
Cretaceous (Klb 9)					
<i>Amberleya spinigera</i>	3	0	-	1.80-3.50	0

<i>Austroaporrhais larseni</i>	1	0	-	2.34	0
<i>"Cassidaria" mirabilis</i>	13	3	0.231	1.54-3.88	3(7) [0.539]
<i>Cryptorhytis philippiana</i>	3	0	-	2.57-2.76	1 (3) [1.000]
<i>Heteroterma? sp.</i>	2	0	-	1.47-2.78	0
<i>Taioma charcotiana</i>	7	0	-	2.35-4.68	0
<i>"Vanikoropsis" arktowskiana</i>	3	1	-	1.90-3.08	0
Bivalves <i>Cucullaea antarctica</i>	5	0	-	3.16-4.60	0
<i>Pycnodonte vesicularis</i>	115	55	0.478	1.13-5.54	17 (35) [0.304]
<i>Eselaevitrigonia regina</i>	34	13	0.382	1.92-5.78	1(2) [0.059]
<i>Oistotrigonia pygoscelium</i>	2	0	-	2.94-3.68	0
<i>Lahillia larseni</i>	30	4	0.133	2.29-5.61	3 (6) [0.200]
Annelids <i>Rotularia (A.) sp.*</i>	67	22	0.328	0.87-2.42	12(27) [0.403]
<i>Klb 7 and 8</i>					
Gastropods <i>Amberleya spinigera</i>	14	1	0.071	0.91-6.03	3 (7) [0.500]
<i>Austroaporrhais larseni</i>	2	0	-	2.26-3.08	0
<i>"Cassidaria" mirabilis</i>	32	10	0.313	1.06-4.00	6(12) [0.375]
<i>Struthiochenopus hurleyi</i>	2	0	0	1.05-1.65	1(2) [0.500]
<i>Taioma charcotiana</i>	10	1	0.100	1.77-4.82	3(6) [0.600]
<i>"Vanikoropsis" arktowskiana</i>	16	1	0.063	1.58-4.27	0 [0.00]
<i>Perissoptera nordenskjoldi</i>	4	0	0	1.05-2.88	0 [0.000]
<i>Cryptorhytis philippiana</i>	5	1		1.26-3.61	0
Bivalves <i>Nucula suboblonga</i>	3	0	-	3.80-3.96	0
<i>Nodenskjoldia nordenskjoldi</i>	14	2	0.143	2.69-4.57	1(2) [0.143]

<i>Cucullaea antarctica</i>	31	6	0.194	1.67-5.78	2(4) [0.129]
<i>Pycnodonte vesicularis</i>	78	42	0.538	0.91-5.56	14 (35) [0.449]
<i>Pulvinites antarcticus</i>	1	0			
<i>Eselaevitrigonia regina</i>	31	11	0.355	1.88-6.41	3(7) [0.226]
<i>Oistotrigonia pygoscelium</i>	15	7	0.467	0.47-2.87	0 [0.000]
<i>Dozyia drygalskiana</i>	10	0	0.000	1.61-3.45	0 [0.000]
<i>Lahillia larseni</i>	2	0	-	3.17-4.42	0
<i>Surobula nucleus</i>	1	0	-	1.00	0
Serpulids <i>Rotularia</i> (A.) sp.*	109	19	0.174	0.62-3.80	1.0 11(26) [0.239]

250

251 ^Prey Effectiveness (defined as the number of incomplete drill holes divided by the total number of
252 drill holes observed in any sample) is calculated for all taxa where there were 10 or more drill holes;
253 † MULT defined as number of holes in multiply drilled specimens over total number of attempted
254 drill holes- = insufficient data; * data for *Struthiochenopus nordenskjoldi* and *S. hurleyi* are pooled
255 and although Macellari (1984) recognises 5 different species of *Rotularia* (*Austrorotularia*) from
256 Seymour Island, they are pooled herein.

257

258 4.1 Drill hole characteristics

259 Unaltered drill holes were circular in plan view with sharp outer edges. There was a
260 continuous range of diameters, from 0.62 to 6.41 mm, across the interval studied. Most
261 drill holes were straight-sided but a few, most notably those on curved shells such as the
262 smaller tubes of *Rotularia*, were more countersunk (i.e., holes with a bevelled edges).
263 Incomplete holes had flat bases. All holes recorded were through shell or tube walls and
264 none of the bivalves attacked were 'edged drilled' (i.e., drilled at the commissure between
265 the valves) in the manner described by Vermeij (1980). None of the drill holes observed

showed signs of having been drilled from the internal surface of the shell or tube (and thus obviously post-mortem). There were no obvious changes in drill hole characteristics over the K-Pg boundary.

4.2 Prey selection

A total of 24 taxa (15 species of bivalves, 8 species of gastropods and 1 genus of serpulid worm) were found to be perforated by at least one drill hole (either complete or incomplete) over the whole study period (Table 1). Some taxa which are well represented in the collections (e.g. the bivalves *Pinna*, *Seymourula*, *Leionucula*, *Entolium*, and *Panopea*, and gastropods such as *Leptomaria* and *Mesalia*) were apparently not drilled.

Analysing the relative numbers of drill holes in different taxa over the four study intervals reveals that for both the pre-extinction zones and the recovery interval the majority of holes were recorded in bivalve prey. Prior to the extinction serpulid worms were also a significant proportion of the prey but not after; only 17 individuals were found in Kplb 10 (only 2 individuals of which were drilled) and it is even possible that these were derived from lower units. Although gastropods were taken in all study intervals, only in the Sobral Formation were they the dominant prey type. The number and variety of these different taxa also changes markedly across the study intervals, with high levels of pre-extinction, with 19 species (8 gastropod, 10 bivalve and 1 serpulid) in Klb 7 and 8 and 13 species (7 gastropod, 5 bivalve and 1 serpulid) in Klb 9, but much fewer in both Kplb 10 (total of 4 species, 1 gastropod, 2 bivalve and 1 serpulid) and the Sobral Formation (total of 7, 2 gastropod and 5 bivalve). Prey taxa may be grouped according to family in order to gain some insight into patterns across the study period where although a single species does not span the total interval it may belong to either a genus or family which is represented in the

driller's diet over longer durations. Table 2 provides the life habit details of these higher taxa which have at least 10 drill holes in the entire data set, and account for >96% of the total number of drill holes studied. The taxa are believed to be either largely infaunal or semi-infaunal inhabitants of soft sediments, and suspension feeders.

Table 2. Inferred life habits for major prey items (based on functional morphology and knowledge of modern taxa; mostly after Macellari (1988)).

Prey type	Inferred life habit
Bivalvia	
Oysters <i>Pycnodonte vesicularis</i> , <i>P. seymourensis</i>	Cemented to small hard substrata (often conspecifics) by part of the left valve, probably at full size, being partly submerged in soft sediment. Frequently found in aggregations
Arcoids <i>Cucullaea ellioti</i> , <i>Cucullaea antarctica</i> , <i>Nordenskjoldia nordenskjoldi</i>	Very shallow non-siphonate burrowers, living with posterior margin more or less parallel to sediment/water interface (Morton, 1981)
Cardioids <i>Lahillia larseni</i> , <i>L. huberi</i>	Very shallow siphonate burrower – some evidence to suggest that posterior margin was exposed above the sediment – water interface
Trigoniids <i>Eselaevitrigonia regina</i> , <i>Oistotrigonia pygoscelium</i>	Very shallow non-siphonate burrowers. Modern trigoniids are rapid burrowers with 'leaping' escape response (Tevesz, 1975)
<i>Dozyia drygalskiana</i>	Medium-sized astartid; likely shallow-burrowing suspension feeder
Gastropoda	
Aporrhoids: <i>Struthiochenopus nordenskjoldi</i> and <i>hurleyi</i> , <i>Austroaporrhais larseni</i> , <i>Perisoptera</i>	Modern aporrhoids are sluggish grazers that live at least part of the year infaunally (Yonge, 1937; Perron, 1978)
Probable neogastropod <i>"Cassidaria" mirabilis</i>	Most likely an active predator (see Crame et al., 2014)
Probable neogastropod: <i>Taioma charcotianus</i>	Most likely an active predator (see Crame et al., 2014)
<i>Amberleya spinigera</i>	Likely epifaunal grazer
<i>"Vanikoropsis" arktowskiana</i>	Considered to be a soft-substrate burrower and inferred to be a drilling predator (Crame et al., 2014)
Serpulids	
<i>Rotularia</i> spp.	Juveniles attached to small hard substrata but there are conflicting suggestions that the adult may have been infaunal (Macellari, 1984) or epifaunal, reclining on a soft bottom (Savazzi, 1995)

4.3 Incomplete drill holes and Prey Effectiveness

Incomplete drill holes occurred throughout the section and were more common in some prey taxa than others. For those taxa for which there were sufficient data to calculate the Prey Effectiveness (PE) metric (Table 1), values ranged from 0.00 in the astartid *Dozyia drygalskiana* in Klb 7 and 8 to 0.538 for the oyster *Pycnodonte vesicularis* from the same interval. All failed drill holes recorded resulted from incomplete penetration; none were observed to have been complete but repaired by subsequent shell deposition by a still living prey as illustrated by Dietl (2000).

There were sufficient data for comparison of the diameter of complete and incomplete drill holes within a particular taxon and time interval in 11 instances. In each of these the mean diameter of incomplete drill holes was smaller than that of those that were complete (Table 3). With a null hypothesis that the mean diameter of complete and incomplete drillholes is equal, applying a one-tailed binomial test, the probability of incomplete drill holes being smaller in 11 samples would be $(0.5)^{11}$ or 0.0005.

Table 3. Comparison of the mean diameters of complete and incomplete holes

Unit	Prey Taxon	Mean diameter of Complete drill holes (mm) [N]	Mean diameter of Incomplete drill holes (mm) [N]
Sobral	<i>Struthiochenopus</i> spp	2.18 [20]	2.09[6]
Kplb 10	<i>Lahillia larseni</i>	3.50[21]	3.37[4]
Klb 9	<i>Lahillia larseni</i>	3.60[26]	3.12[5]

	<i>Eselaevitrignia regina</i>	3.30[21]	3.05[13]
	<i>Pycnodonte vesicularis</i>	3.67[38]	2.85[34]
	<i>Rotularia</i> spp.	1.64[42]	1.46[25]
Klb 7 and 8	<i>Eselaevitrignia regina</i>	3.67[20]	3.01[10]
	<i>"Cassidaria" mirabilis</i>	2.57[19]	1.89[10]
	<i>Cucullaea antarctica</i>	3.70[23]	2.86[6]
	<i>Pycnodonte vesicularis</i>	2.84[37]	2.50[42]
	<i>Rotularia</i> spp.	1.76[89]	1.50[19]

Lahillia larseni is the only taxon for which there were sufficient data to test whether there was a change in PE over the K-Pg boundary. The PE is higher in the recovery interval fauna, i.e. Kplb 10, (0.148) than in the pre-extinction beds (0.133) but this increase is not statistically significant ($p = 0.53$ by chi-squared test). The aporrhaid, *Struthiochenopus* spp was the only taxon for which there was a statistically significant change in PE between any of the study intervals and with an increase between the Kplb 10 (PE = (0.071) and the Sobral Formation (PE = 0.200) ($p = 0.02$ by Chi-squared).

4.4 Multiple drill holes (MULT)

Multiple drill holes (MULT) were recorded in a number of taxa across all the studied stratigraphic intervals (Table 1). Although both MULT and PE may be seen as measures of prey defence against a drilling predator, the two are not correlated in our data ($p=0.744$). The only taxon/stratigraphic intervals for which there were more than 10 drill holes and a MULT of zero were recorded for *Dozyia*, *Oistotrigonia* and "*Vanikoropsis*" *arktowskiana* (all units Klb 7 and 8). MULT values of higher than 0.2 were recorded in the bivalves *Lahillia* (units Klb 9 and Kplb 10), *Eselaevitrighonia* (units Klb 7 and 8) and *Pycnodonte* (units Klb 7 and 8 and Klb 9, and Sobral Fm), the gastropods *Struthiochenopus* (Sobral Fm), "*Cassidaria*" (units Klb 7 and 8 and 9), *Amberleya* (units Klb 7 and 8) and *Taioma* (units Klb 7 and 8) and also for serpulids in units Klb 7 and 8 and 9. MULT is generally high for molluscan taxa and serpulids from unit Klb 9.

As with PE, *Lahillia larseni* was the only taxon with sufficient data for which it was possible to investigate for differences in MULT on either side of the K-Pg boundary. In this instance there was significant increase in the metric above the boundary (3% by chi-squared test). There was also a significant increase in MULT between Unit 10 and Sobral in the aporrhaid *Struthiochenopus* spp data ($p = 0.01$ by chi-squared test).

Most multiply drilled individuals had two holes, but three was not uncommon in some individuals of *Pycnodonte* and a single individual had four. Most of the multiple holes in the oysters were all in the left valve. For most taxa and individuals with multiple attempts there was at least one incomplete one and in most of these instances the two or more holes were of notably different diameter. There were, however, a number of instances where a prey item was penetrated by more than one complete hole. This was particularly common in *Struthiochenopus* where six out of eight multiply drilled individuals

(amalgamated from all stratigraphic intervals) had more than one complete hole, though it was also frequent in the oyster *Pycnodonte*.

4.5 Drill hole positioning and site selection

As might be anticipated for equivalve orthothetic bivalves such as *Lahillia*, arcoids and trigoniids, there were no statistically significant differences between numbers of drill holes in right and left valves (chi-squared test - $p > 0.05$ in all cases). However, for the markedly inequivalve and pleurothetic oysters, there was a clear preference for drilling the 'lower' left valve (chi-squared test - $p < 0.001$) in all units. The position of drill holes on most bivalve taxa was not random. For *Lahillia larseni*, *Eselaevitrigonia regina* and all of the arcoids there were statistically significant preferences for drilling the posterior dorsal sector of the shell (chi-squared test - $p < 0.001$ in all cases). Moreover, for the arcoids *Cucullaea antarctica* and *Nordenskjoldia nordenskjoldi* there was a preference for drilling through the ligament platform, often at the join between the two valves (Fig. 2A). Additionally, there was a marked tendency for drilling the central region of oyster valves (chi-squared test - $p < 0.0001$ at all stratigraphic levels), though with no particular preference for the adductor muscle scar itself.

Most drill holes in gastropod prey were placed in the most recently formed whorl but with no clear sign of consistent placing in relationship to the aperture (although such a pattern may be obscured by frequent damage to that region making aperture position hard to establish for a complete animal). For the serpulid, *Rotularia*, drill holes were recorded in all analysed sectors but there was a pronounced preference for drilling in that adjacent to the aperture (chi-squared test- $p < 0.001$) (Fig. 2D), but no statistically significant preference between dorsal and ventral surfaces for each segment (chi-squared test - $p > 0.05$).

4.6 Drill hole size analysis

The range of drill hole sizes recorded in individual prey type and stratigraphic units are shown in Table 1. A 2-tailed Student's T test was used to compare the sizes of drill holes in each time interval. Although the mean size of holes in the Sobral Formation (2.37 mm) is significantly smaller ($p < 0.003$ in all instances) than those in all the other units, and the mean size of those in Klb 7 and 8 (2.78 mm) is smaller than those in unit Klb 9 (3.25 mm) ($p < 0.001$), the range of drill hole sizes in all units is similar. The minimum and maximum diameters recorded in each unit is less than 0.9 mm and greater than 4.6 mm.

In order to explore whether there was any indication of size selection within a prey taxon we examined the relationship between drill hole diameter and prey size (length for bivalves, height for gastropods and width of serpulids) in taxa for which there were sufficient data (note that not all specimens were complete enough to measure prey size). Because we had found that incomplete drill holes were frequently significantly smaller than complete ones (see above), we restricted our analysis to complete holes. Firstly we investigated data within the two Cretaceous intervals (Klb 7 and 8 and Klb 9). There was a significant positive correlation between drill hole and individual prey size for only the unit Klb 9 *Pycnodonte* (one tailed test, $p = 0.001$) and units Klb 7 and 8 *Rotularia* (one tailed test, $p < 0.001$). There was insufficient data to test this relationship for "*Vanikoropsis*" in separate time bins, but an amalgamation of the Cretaceous data revealed a positive correlation (one tailed test, $p = 0.041$). Perhaps most surprising, there was a negative correlation for prey size and drill hole diameter in *Nordenskjoldia nordenskjoldi* from units Klb 7 and 8 (one tailed test, $p = 0.02$), although the sample size was low ($n = 10$ complete drill holes).

The size range of drilled individuals for each prey taxon was rather narrow. Because of the size of the task and the incompleteness of many specimens no attempt was made to measure the size of undrilled molluscan prey, but for *Rotularia* the mean sizes of drilled individuals (19.1 mm, n = 146) was significantly larger than for undrilled (17.7 mm; n=2353) (Mann-Whitney U test $p<0.01$). It is striking that *Rotularia* was a relatively small prey item and was penetrated by drill holes at the lower end of the range of diameters recorded across the study. These facts suggest an alternative way to explore the issue of prey size selection by ranking prey. Although it is difficult to rank extinct prey in terms of their flesh yield, a simplified approach of plotting the size of all prey items (length for bivalves, height for gastropods and width for worms) against drill hole diameter within the four stratigraphic intervals reveals for each of them that there is a significant positive relationship (Table 4).

Table 4. Correlation coefficients and significance levels for diameter of complete drill holes vs largest dimension of each prey item in each of the stratigraphic intervals.

Stratigraphic Interval	N	r^2	p
Sobral Formation	26	0.3598	<0.001
Unit Kplb 10 –	31	0.2339	<0.0059
K-Pg Boundary			
Unit Klb 9	139	0.0385	<0.0001
Units Klb 7 and 8	179	0.0786	<0.00014

5. Discussion

The highly distinctive trace fossils reported here are good evidence that predatory drilling was not an uncommon fate for both shelly molluscs and serpulid worms in Antarctic shallow water marine communities during both the end-Cretaceous and in the immediate aftermath of the K-Pg mass extinction. As we have a comparatively large data set of some 759 drill holes effectively from a single site, they allow us to assess the impact of the K-Pg event on the patterns of drilling predation in the immediate region and provide useful comparison with previous studies of lower latitude localities over the same time interval.

5.1 Likely driller

It is a well known paradox that although the recognition of the predatory nature of drill holes in both modern death assemblages and fossil material is relatively uncontroversial, assigning a particular predatory taxon as responsible is highly equivocal (Bromley, 1981). Several higher taxa, including a variety of gastropods, octopods, nematodes and turbellarian worms, are known to drill holes in their shelly prey (Kabat, 1990; Kelley and Hansen, 2003). However, the drill holes described in this paper are relatively large (diameters ranging from 0.62 to 6.41 mm), much bigger than those associated to date with turbellarians, nematodes and most octopods (Carriker, 1981; Kabat, 1990; Todd and Harper, 2011) and penetrate sizeable prey. As such they conform well to the expectations for those drilled by gastropods (Carriker, 1981; Bromley, 1981; Kabat, 1990).

The majority of victims of these drilling attacks were predominantly either sessile or slow moving animals and mainly characterised as infaunal or semi-infaunal soft sediment dwellers, mostly with suspension feeding life habits. Although most of the bivalves were fully infaunal and there is a tendency for these to have been attacked at the posterior end (i.e. closest to or even above the sea floor), nearly 25 % of all drill holes were in the

gryphaeid oysters, *Pycnodonte*. These oysters likely lived semi-submerged on their left valves in the soft sediment and most holes were recorded on the 'lower' left valve which is probably consistent with being attacked from underneath as noted by Dietl (2002) for Paleocene congeners from the USA. Together these observations point to a predominantly shallow infaunal predator, perhaps capable of foraging at the surface as well.

The predominantly infaunal/semi-infaunal nature of prey, the handling preferences and several (but not all) aspects of the drill hole morphology suggest a naticid gastropod driller (Carriker, 1981; Bromley, 1981; Kabat, 1990). Other studies of drilling predation from either Late Cretaceous or early Paleogene sediments show that the holes are coeval with well accepted naticid records elsewhere in the world (e.g. Kelley and Hansen, 1993; Harries and Schopf, 2007; Mallick et al., 2013). However, despite the abundance of the naticids, *Amauropsis* and *Euspira* higher up the geological sequence in the Eocene La Meseta Formation (Crame et al., 2014), and whose predatory drill holes have been recognised in a range of shelly prey (Aronson et al., 2009), there are no records, despite extensive collection efforts, of unequivocal naticids at the stratigraphic levels studied here. However, following Crame et al. (2014) we consider that the only plausible gastropod culprit is "*Vanikoropsis*" *arktowskiana*. This enigmatic taxon has an exact temporal coincidence with the drill holes ranging from the base of the López de Bertodano Formation (to the top of the Sobral Formation on Seymour Island, including the recovery unit (Crame et al., 2014). Stilwell et al (2004) referred this taxon to *Vanikoropsis* Meek, 1876 of the caenogastropod family Vanikoridae. Crame et al. (2014), however, revert to the original placement by Wilckens (1910), partly on the basis of co-occurrence with drill holes, to favouring a naticid affinity and suggest that in the future the taxon should be placed in a new genus of the family Naticidae. Although the drill holes presented here do not share some of the well-

documented characteristics of classic naticid holes, such as having a central raised boss (rather than flat) on the floor of incomplete holes and many are not properly countersunk, our findings here support this view. It should be noted that there are no muricid gastropods (the other major clade of gastropods which drill molluscs albeit largely on hard substrates) in the fauna.

5.2 Changes in potential prey over the K-Pg

Regardless of the exact identity of the predator, our data provide an opportunity to examine patterns in predator-prey interactions across this major biotic event. If we are correct in identifying a single drilling predator on both sides of the boundary our analysis is strengthened because there is no mixed signal conflating the activities of different predators with different preferences and behaviours (Casey et al., 2015). We preface the following remarks with our considered opinion that there is only one mass extinction horizon within the latest Cretaceous – earliest Paleogene succession of Seymour Island. Although the possibility of a double extinction has been suggested by statistical analyses (Tobin et al., 2012; Tobin, 2017), we could find no evidence for it in the field nor when the confidence intervals on the range data are considered. As stated in Witts et al. (2016), the topography of the boundary interval in our study area is such that exposure varies greatly in the uppermost Maastrichtian. The last really good exposure beneath the K – Pg is a dip-slope at approximately -45m, and very large collections have now been made from this. Thereafter exposure is largely scarp-face up to the K-Pg and collections from this level are much more restricted. But confidence interval analysis indicates that many taxa recorded from the -45m level would in fact extend up to the K- Pg and there is no marked pre-extinction in either benthic or pelagic taxa (Witts et al., 2016). The actual K – Pg boundary is quite clearly

marked by a stratigraphic hiatus at the base of the lower glauconite which can be traced, albeit intermittently, along the 7 km of strike.

Our data demonstrate a sharp reduction in prey diversity across the K–Pg boundary in Antarctica. Recent studies have shown that when benthic molluscan taxa from the topmost 50 m of Maastrichtian strata (i.e. topmost unit Klb 9) are compared with unit Kplb 10 then there is a species level extinction of approximately 60% across the K–Pg (Witts et al., 2016). However, if a comparison is made using the whole of unit Klb 9 (33 benthic molluscan species) and unit Kplb 10 (8 species) then the extinction level rises to 75%; the inclusion of three range-through taxa reduces these figures to 56% and 67%, respectively. Regardless of which level is cited, the important point to emphasise is that prey choice is drastically reduced in Kplb 10 (the recovery interval). Of the eight benthic molluscan species recorded directly from it only three, the bivalves *Lahillia larseni* and *Cucullaea ellioti*, and gastropod *Struthiochenopus hurleyi*, can be described as abundant (Witts et al., 2016). The serpulid *Rotularia* is also almost completely absent from this interval (Zinsmeister et al., 1989; Stilwell et al., 2004; Witts et al., 2016).

Although a 60% or even greater level of extinction across the K–Pg boundary might prove fatal for a single predator such as “*Vanikoropsis*” *arktowskiana*, it is important to emphasise that three of those taxa that remain, i.e. *Lahillia larseni*, *Cucullaea ellioti* and *Struthiochenopus hurleyi*, are extremely abundant in unit Kplb 10 (Witts et al., 2016) and it may well be that opportunistic taxa play an important role in maintaining the volume of prey source following a mass extinction event (Hansen et al., 2004).

It also has to be borne in mind that the K–Pg boundary is a time of significant change in the overall composition of benthic marine faunas, with bivalve-dominated ones

throughout the latest Cretaceous giving way to gastropod-dominated ones in the earliest Paleocene (Hansen, 1988; Sepkoski, 2002; Stilwell, 2003). This is a truly global phenomenon that is due to the rise of benthic marine predators in general and predatory neogastropods in particular. The Seymour Island sedimentary succession documents a very steep rise in the number of neogastropod taxa between the K–Pg boundary and the Middle Eocene (Crame et al., 2014).

It might be predicted that potential prey taxa that survive or flourish after mass extinctions will be less well armoured, as evidenced by the expression of morphological features such as shell thickness and ornamentation (Vermeij, 1994). Although we have not collected specific data on these traits, there is no obvious evidence of such morphological differences between the post and pre-extinction faunas of Seymour Island, in particular when comparing congeners or conspecifics which traverse the extinction. In this respect our findings echo those of Hansen et al. (1999) in their study of US Coastal Plain molluscs.

5.3 Actual prey choice

Our evidence suggests that at each stratigraphic level examined the driller had a catholic diet. It must be emphasised that the range of prey taken may have been even broader if it included soft-bodied taxa that have not been preserved or taxa that were subdued without drilling. Prey types across the study interval are broadly similar, i.e. slow moving/sedentary taxa living in or on soft bottoms. The exact nature of the prey varies depending on stratigraphic level and probably also reflects patchiness within the environment. This is particularly so in the latest Maastrichtian units Klb 8 and 9 where taxa such as *Rotularia* and *Pycnodonte* occur locally in high numbers (Macellari (1984, 1988).

Slow moving gastropod predators might be expected to be strongly influenced by such patchiness rather than having an ability to hunt out favoured prey (Harper, 2016).

Only a few species survive over the entire study interval (e.g. *Lahillia larseni*, *Pycnodonte vesicularis* and “*Vanikoropsis*” *arktowskiana*) but for only *L. larseni* are there sufficient data to analyse patterns in drilling behaviour in a single prey taxon over the K-Pg event. Some prominent prey taxa before the mass extinction either disappear regionally in that event (e.g. trigoniid bivalves are restricted to Australasia only following the mass extinction; Darragh, 1986), or reduce dramatically in number (serpulid worms). Both trigoniids and serpulids are prominent in the pre-extinction prey lists. Although the mass extinction removes certain species, in some cases they are replaced in unit Kplb 10 and Sobral Formation by congeners and confamilials. It is striking that although drilled aporrhaid gastropods were present throughout the study period, they are a much greater proportion of the total number of drill holes in the two intervals succeeding the mass extinction. This would seem to be a direct consequence of the very low availability of shallow – burrowing infaunal bivalves in these levels.

5.4 Frequency of attack

Although other studies have determined drilling frequencies across mass extinction events (Kelley and Hansen, 1993; Kelley et al., 2006) we have chosen not to do so because although the Seymour Island fossils are well preserved, they are frequently not whole and they were not collected as bulk samples. Another complication of such measures is that they ignore the differential effect that extinction itself might have had on taphonomy. Vermeij et al. (1989) have persuasively pointed out that the co-occurrence of active crushing predators at a site effectively removes undrilled dead individuals from any survey, thereby

inflating calculated drilling frequencies. Major changes in either the crustacean or vertebrate predator fauna at the K-Pg event may have significantly altered the proportions of drilled and undrilled individuals in the fossil record. The Cretaceous sections of Seymour Island yield frequent mosasaur material (Martin and Crame 2006) and it is not impossible that for pre-extinction large molluscs (e.g. *Lahillia*) these would have been effective crushing predators, thus perhaps over emphasizing the frequency of drill holes. We did not undertake a systematic survey of the collections for repaired breakage but noted that repaired apertural breaks, similar to those seen in Allmon et al. (1990), indicate peeling predation both pre- and post-extinction.

Recent evidence has suggested that the frequency of drilling predation by naticid gastropods decreases with increasing latitude along the east coast of South America (Visaggi and Kelley, 2015). Despite our lack of frequency data it is possible to demonstrate that at this high latitude site (~ 65°S) predatory drilling appears to be not uncommon at this time, as in the late Paleocene and Eocene (Aronson et al., 2009). Although the Neogene fossil record of Antarctica is very incomplete, it is interesting to note that naticid genera such as *Falsilunatia* and *Amauropsis* are relatively common in the Southern Ocean at the present day (Dell, 1990).

5.5 Patterns of prey handling

Modern naticid species are known to be highly selective in terms of both prey size and site of attack, which is prey taxon specific (Kitchell et al., 1981; Boggs et al., 1984). These studies also demonstrate that drill hole diameter can be used as a proxy of predator size.

Despite a varied diet, the Seymour Island driller showed consistent handling with prey taxon-specific siting of drill holes in many instances. Much of the placement constancy recorded here probably reflected the ease with which a shallow infaunal predator could attack the prey, hence the preference for the posterior part of burrowing bivalves and the underside of semi-infaunal oysters but stereotypic placement of drill holes also implies familiarity of handling and drilling particular prey items. Interesting examples are the apparent preference for drilling through the ligament platform in arcoids and next to the aperture in *Rotularia*.

There is evidence of size selectivity by the driller. Smaller predators, as shown by smaller diameter drill holes, took smaller prey types. A similar case of the drill holes in serpulid prey being statistically smaller than those drilled in larger bivalves is reported by Klompmaker (2012) for a Pliocene shallow marine fauna from the Netherlands. There is also evidence in the Seymour Island *Rotularia* that a size refuge was reached whereby larger individuals avoided drilling. Incomplete drill holes were significantly smaller than complete ones suggesting that smaller, perhaps more inexperienced, drillers were more prone to failure than larger ones. This can be taken as further evidence of size selectivity.

Both handling stereotypy and size selectivity may be taken as evidence of familiarity by the predator and our data suggest that despite changing prey availability, the driller maintained such patterns through the study interval. Thus there is no evidence at this site to support the hypothesis that prey selectivity decreases after mass extinctions.

5.6 Failure

Failed predation attempts are common for most predator-prey systems and unsuccessful predation is important in promoting defensive adaptations (Vermeij, 1982). Our data show that incomplete drill holes occur throughout the section and in most prey taxa. High levels of PE were found in taxa with notable defensive adaptations, such as relatively thick shells (e.g. *Pycnodonte* and *Lahillia*) or those with active escape responses, for example leaping in trigoniids (Tevesz, 1975). Failed drill holes were in all cases examined smaller than complete holes in the same prey items, and in large enough data sets significantly so thereby implying that perhaps over-ambition and mismatch of prey and predator size.

Defensive adaptations which are active (such as leaping or swimming) or which may involve laying down additional structures (such as thick shells or spines) have an additional metabolic cost. Vermeij (1987) proposed that highly escalated, well defended prey are more liable to extinction events associated with failures in food supply because of the relative metabolic costs of their life styles. It might be predicted, consequently, that predation success should increase in the aftermath of such events because surviving taxa were less well-defended. In the context of this study then, one might expect to see a reduction in Prey Effectiveness (PE) values over the K-Pg. Alternatively, a change in PE across a mass extinction might suggest changes in competition and availability of prey (Dietl et al., 2004; Hutchings and Herbert, 2013). However, similarly to Kelley et al. (2001) for the US Coastal Plain, our data reveal no statistically significant change in PE over the mass extinction at this site to be explained by either hypothesis. The only significant change in PE recorded anywhere in our data set was for an increase in *Struthiochenopus* prey between

the recovery and the Sobral units. While perhaps this supports the notion of better defended prey emerging after the recovery, the data are limited to this taxon.

The phenomenon of multiple gastropod drill holes in prey items has been addressed by several authors (Kitchell et al., 1986; Kelley and Hansen, 2007). It is evident that the presence of several holes in any individual prey item may reflect a range of causes, for example interruption and resumption of drilling by a single predator, group attacks by a number of drillers (e.g. Brown and Alexander, 1994), or possession of highly effective prey defences (for example the organic sheets in corbulid bivalves (Lewy and Samtleben, 1979). MULT may be seen as a metric of prey effectiveness in only the last case. In our data high values of MULT are associated with particular taxa, many of which have obvious defences; however, there is no correlation between PE and MULT. One factor that may be important here is that the frequency of MULT is likely to be in part controlled by prey longevity; the longer a prey lives the more likely it is to be attacked on multiple occasions throughout its life. Although longevities have not been determined for all the taxa concerned, it is well known that high latitude taxa tend to be more long-lived (Moss et al., 2017). It is interesting to note that the values of MULT recorded in our study are generally higher than those recorded for the Cretaceous faunas on the US Coastal Plain (Kelley et al., 2001). Despite the difficulty of interpreting MULT it is worth noting that for *Lahillia* there is a significant increase over the mass extinction and also between unit Kplb 10 and the Sobral Formation for aporrhoids.

5.7 Cannibalism

If we are correct that “*Vanikoropsis*” *arktowskiana* is the driller, then there is evidence of cannibalism throughout the section with the exception of in unit Kplb 10.

Intraspecific predation is widespread across extant animal groups and may have profound importance to both ecological relationships and evolution (Polis, 1981). Cannibalism, at both family and species level, is well known in modern and fossil naticid gastropods (Kitchell et al., 1981; Kelley, 1991; Kelley and Hansen, 2007; Chattopadhyay et al., 2014, Brezina et al., 2016). Its significance is a matter of debate; while it may be interpreted as a perfectly normal prey selection (Kitchell et al., 1981; Chattopadhyay et al., 2014; Brezina et al., 2016), others have suggested it might be due to lack of other prey availability (Taylor, 1970), or predator ineptitude (Stanton and Nelson, 1980).

Our data on this interaction are limited, with drill hole numbers being highest pre-extinction in Klb 7 and 8. They show good evidence of size selectivity and prey effectiveness is relatively low and the range of drill hole diameters (1.10 to 4.27 mm) indicates that this was a behaviour that was persistent over a range of ontogenetic ages and not necessarily practiced by only older individuals as was found by Chattopadhyay *et al.* (2014).

6. Conclusions

Our data on predator-prey interactions over the K-Pg boundary in Antarctica show the activities of a drilling predator, probably "*Vanikoropsis*" *arktowskiana*, was capable of attacking a diverse range of molluscs and serpulid worms associated with soft sea floors. Although the choice of prey items changed over the time interval studied, most notably restricted after the mass extinction, various metrics of attack success and handling behaviour suggest that, despite this major biotic crisis, it was 'business as usual'.

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